Brachiopods across the Ordovician–Silurian boundary

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Synopsis

Most of the late Ordovician brachiopod superfamilies also extend into the early Silurian, although the Gonambonitacea become extinct at or near the Ordovician–Silurian boundary and the earliest Cyrtiacea are found very close above it. Faunas close to the boundary are reviewed and listed, and the Hirnantian faunas of the latest Ordovician are found to be richer than the earliest Silurian Rhuddanian faunas in both abundance and diversity.

Introduction

At the time the Treatise on Invertebrate Paleontology brachiopod volume (Williams *et al.* 1965) was written, 44 brachiopod genera were recorded with ranges spanning the Ordovician–Silurian boundary, and in addition there were various families and subfamilies whose ranges spanned the boundary even if the recorded ranges of individual genera within them did not. The superfamilies involved are the Lingulacea, Trimerellacea, Discinacea, Craniacea, Orthacea, Enteletacea, Tripleciacea, Eichwaldiacea, Plectambonitacea, Strophomenacea, Davidsoniacea, Chonetacea, Porambonitacea, Pentameracea, Rhynchonellacea, Atrypacea and Athyridacea—a list which in itself demonstrates the morphological variability and diversity of the phylum in Ordovician–Silurian boundary times.

However, rather than review each family, genus or species in turn here, it is more relevant to consider the brachiopod faunas actually recovered from strata near the boundary. In general the middle Ashgill was a period of great diversity among the brachiopods, but this diversity was reduced when the Rawtheyan endemic faunas, for example of North America (the late Richmondian) and Europe (e.g. the Boda Limestone of Sweden) gave way to the more cosmopolitan, and hence in total less diverse, faunas of Hirnantian times. Similarly, the profound effect of the Ordovician–Silurian boundary glacial episode made the subsequent recovery and build-up of the brachiopod faunas rather slow, and thus, even where the earliest Llandovery time is represented by rock (and not by the usual unconformity), the numbers and more particularly the diversity of the brachiopod faunas were rather poor.

Latest Ordovician and earliest Silurian brachiopods

In the following lists the records are reproduced of reliable determinations from relatively recent papers on brachiopods of Hirnantian and early Rhuddanian ages respectively. In most cases they are as the original authors determined them, but with 'aff.' or 'cf.' omitted, and sometimes with genera or species updated by subsequent works. They are from the following authors and localities: A, uppermost Ellis Bay and lowermost Becscie Formations, Anticosti Island, Canada (Cocks & Copper 1981); B, Kosov Formation, Bohemia, Czechoslovakia (Marek & Havlíček 1967; Havlíček 1977); D, Durben Horizon, Kazakhstan, USSR (Nikitin *et al.* 1980); E, Lower Edgewood Group, Oklahoma, USA (Amsden 1974); G, High Mains Sandstone and Lady Burn Formation, Girvan, Scotland (Cocks & Toghill 1973; Harper, this volume); H, St Martin's Cemetery Horizon, Haverfordwest, Wales (Cocks & Price 1975); I, Hol Beck, England (Temple 1965); K, Kildare, Ireland (Wright 1968); L, Bronydd Formation, Llandovery, Wales (Cocks *et al.* 1984); M, *persculptus* and *acuminatus* Zones, Mirny Creek, north-east USSR (Koren *et al.* 1983); O, Langøyene and Langåra Formations, Oslo–Asker district, Norway (Brenchley & Cocks 1982; Cocks 1982) and Myren Member (Baarli & Harper 1986); P, Unit 5, White Head Formation, Percé, Québec, Canada (Lespérance & Sheehan 1976,

1981); R, Varbola Formation, Estonia, USSR (Rubel 1970); S, Stawy, Poland (Temple 1965); V, Dalmanitina Beds, Västergotland, Sweden (Bergström 1968); W, Hirnant Beds, Wales (Temple 1965); X, Hirnantian Beds, Keisley, England (Temple 1968); Y, Kuanyinchiao Beds, Yichang, China (Rong 1984*a*); Z, Artchalyk and Minkutchar Beds, Zeravshano–Gissar section, Altai Mountains, USSR (Nikiforova 1978).

The latest Ordovician (Hirnantian) records from these localities are as follows:

Lingulacea: *Lingula* sp. H, O; *Lingulella* sp. I, S; *Palaeoglossa* sp. V; *Craniops/Paracraniops* sp. H, O, V, X.

Discinacea: *Trematis norvegica* Cocks O; *Orbiculoidea concentrica* (Wahlenberg) H, V, S; *Orbiculoidea* sp. O.

Craniacea: *Acanthocrania* sp. O, X; *Philhedra grayii* (Davidson) X; *Philhedra* sp. H, V; *Philhedra? stawyensis* Temple I, S; *Philhedrella cribrum* Temple X; *Philhedrella* sp. A, O.

Orthacea: *Comatopoma sororia* Marek & Havlíček B; *Comatopoma* sp. O; *Dolerorthis intermedius* Nikiforova M; *Dolerorthis praeclara* Temple X; *Dolerorthis savagei* Amsden E; *Dolerorthis* sp. O; *Geraldibella bella* (Bergström) M, V; *Geraldibella giraldi* (Bancroft) H; *Giraldibella subsilurica* (Marek & Havlíček) B; *Glyptorthis* sp. G, O; *Hesperorthis* sp. M, O; *Nicolella* sp. O; *Orthostrophella* sp. E; *Plaesiomys* sp. G; *Platystrophia* sp. E, G, O; *Skenidioides scoliodus* Temple X; *Skenidioides* sp. H, O; *Toxorthis mirabilis* Rong Y; *Toxorthis proteus* Temple X.

Enteletacea: *Dalmanella biconvexa* Williams H; *Dalmanella cicatrica* Nikitin D; *Dalmanella edgewoodensis* Savage E; *Dalmanella pectinoides* Bergström B, V; *Dalmanella testudinaria* (Dalman) A, B, H, I, K, M, O, P, S, V, W, Y; *Dicoelosia* sp. E, X; *Diceromyonia? sera* Amsden E; *Draborthis caelebs* Marek & Havlíček B, V, X, Y; *Drabovia agnata* Marek & Havlíček B; *Drabovia westrogothica* Bergström V; *Drabovia* sp. O, X; *Dysprosorthis sinensis* Rong Y; *Epitomyonia* sp. O; *Hirnantia noixella* Amsden E; *Hirnantia sagittifera* (M'Coy) B, D, G, H, I, K, M, O, P, S, V, W, X, Y; *Hirnantia* sp. A; *Horderleyella bouceki* (Havlíček) S, W; *Horderleyella fragilis* Bergström V; *Isorthis* sp. M; *Kinnella kielanae* (Temple) B, P, S, V, W, X, Y; *Leptoskelidion loci* Cocks O; *Leptoskelidion septulosum* Amsden E; *Mendacella*? sp. E; *Mirorthis mira* Zeng Y; *Onniella kalvoya* Cocks O; *Onniella? yichangensis* Zeng Y; *Paucicrura* sp. O; '*Pionodema*' *retusa* Temple X; *Ravozetina rava* Marek & Havlíček B; *Reuschella inexpectata* Temple X; *Trucizetina subrotundata* Havlíček B; *Trucizetina yichangensis* Zeng Y; *Visbyella*? sp. [=*Kayserella* sp. nov. of Temple] X.

Gonambonitacea: *Kullervo*? sp. O.

Tripleciacea: *Cliftonia psittacina* (Dalman) B, H, K, O, V; *Cliftonia obovata* Chang Y; *Cliftonia tubulistriata* (Savage) E; *Cliftonia* sp. D, M; *Onychoplecia* sp. X, Y; *Oxoplecia* sp. O; *Triplesia protea* Oradovskaya M; *Triplesia sanxiaensis* Zeng Y; *Triplesia* sp. O.

Plectambonitacea: *Aegiromena convexa* Chang Y; *Aegiromena durbenensis* Nikitin D; *Aegiromena ultima* Marek & Havlíček B, Y; *Aegiromena* sp. X; *Anisopleurella novemcostata* Nikitin D; *Chonetoidea papillosa* (Reed) H; *Eochonetes* sp. G; *Eoplectodonta nesnakomkaensis* Oradovskaya M; *Eoplectodonta rhombica* (M'Coy) O; *Eoplectodonta oscitanda* Cocks O; *Eoplectodonta* sp. D; *Leangella cylindrica* (Reed) O, V; *Rugosowerbyella ambigua* (Reed) D; *Sampo* sp. O; *Sericoidea*? O.

Strophomenacea: *Aphanomena parvicostellata* Rong Y; *Aphanomena schmalenseei* Bergström V; *Biparetis paucirugosus* Amsden M; *Eopholidostrophia* sp. G; *Eostropheodonta bublitschenki* Nikitin D; *Eostropheodonta hirnantensis* (M'Coy) including *E. lucavica* and *E. siluriana* A, B, G, I, K, M, O, P, S, V, W; *Eostropheodonta whittingtoni* Bancroft H; *Katastrophomena* sp. O; *Kjaerina*? sp. O; *Kjerulfina*? sp. V; *Leptaena aequalis* Amsden M; *Leptaena martinensis* Cocks H; *Leptaena rugosa* Dalman B, D, V; *Leptaena* sp. E, O; *Leptaenopoma trifidum* Marek & Havlíček B, D, K, V, Y; *Paromalomena polonica* (Temple) B, D, I, S, X, Y; *Rafinesquina*? *latisculptilis* (Savage) E, M; *Rafinesquina stropheodontoides* (Savage) E; *Rafinesquina ultrix* Marek & Havlíček B, D; *Rafinesquina urbicola* Marek & Havlíček B, D; *Titanomena grandis* Bergström V.

Davidsoniacea: *Coolinia convexa* (Savage) E; *Coolinia dalmani* Bergström A, O, V; *Coolinia propinqua* (Meek & Worthen) E; *Coolinia* sp. M, Y; *Fardenia comes* Marek & Havlíček B; *Fardenia* sp. G, X.

Porambonitacea: *Parastrophinella gracilis* Oradovskaya M; *Parastrophina* sp. O.

Pentameracea: *Brevilamnulella kjerulfi* (Kjaer) O; *Brevilamnulella thebesensis* (Savage) E, M; *Brevilamnulella undatiformis* Rozman M; *Holorhynchus giganteus* Kjaer O; *Tcherskidium unicum* (Nikolaev) M.

Rhynchonellacea: *Dorytreta* sp. Y; *Hypsiptycha* sp. G; *Rostricellula* sp. G, O; *Rhynchotrema*? sp. M; *Stegerhynchus concinna* (Savage) E, M; *Stegerhynchus*? sp. E, O; *Thebesia admiranda* Oradovskaya M; *Thebesia scopulosa* Cocks O; *Thebesia thebesensis* (Foerste) E.

Atrypacea: *Eospirigerina gaspeensis* (Cooper) M; *Eospirigerina prisca* Oradovskaya M; *Eospirigerina putilla* (Hall & Clarke) E; *Eospirigerina sublevis* Rozman M; *Eospirigerina* sp. G, O; '*Homoeospira*'

fiscellostriata Savage E; *Plectatrypa* sp. M; *Protatrypa* sp. X; *Protozyga gastrodes* Temple X; *Zygospira fallax* Marek & Havlíček B; *Zygospira* sp. O.

Athyracea: *Cryptothyrella crassa* (J. de C. Sowerby) *incipiens* Williams G, H, K, Y; *Cryptothyrella ovoides* (Savage) E; *Cryptothyrella terebratulina* (Wahlenberg) M; *Cryptothyrella* sp. B, X; *Hindella cassidea* (Dalman) O, ?P, ?A; *Hyattidina* sp. M; *Plectothyrella crassicostis* (Dalman) [ex *platystrophoides* Temple] B, I, K, P, S, V, W, Y; *Plectothyrella*? *mirnyensis* Oradovskaya M.

Eichwaldiacea: *Dictyonella* sp. E.

The earliest Silurian (lower part of the Rhuddanian) records from these localities are:

Lingulacea: *Lingula* sp. G.

Discinacea: *Orbiculoidea* sp. H.

Orthacea: *Dolerothis plicata* (J. de C. Sowerby) O; *Dolerorthis sowerbyiana* (Davidson) L; *Dolerorthis* sp. O, R; *Giraldiella* sp. L, Z; *Hesperorthis imbecilla* Rubel R; *Platystrophia* sp. R; *Schizonema* sp. L, O; *Ptychopleurella* sp. R; *Skenidioides scoliodus* Temple M; *Skenidioides woodlandensis* Reed O; *Skenidioides* sp. H, L, O.

Enteletacea: *Dalejina* sp. R; *Dicoelosia osloensis* Wright O; *Dicoelosia* sp. L; *Draborthis*? sp. M; *Epitomyonia* sp. O; *Fascifera* sp. O; *Howellites* sp. O; *Isorthis neocrassa* Nikiforova Z; *Isorthis prima* Walmsley O; *Isorthis* sp. A; *Kinnella* sp. O; *Onniella mediocra* Rubel R; *Ravozetina* sp. L, O; *Resserella* sp. H, L; *Reuschella* sp. O; *Visbyella* sp. L.

Tripleciacea: *Triplesia* sp. L, O.

Plectambonitacea: *Aegiria norvegica* Öpik O; *Anisopleurella* sp. L; *Anisopleurella gracilis* (Jones) H; *Eoplectodonta duplicata* (J. de C. Sowerby) L, O; *Eoplectodonta* sp. H; *Leangella scissa* (Davidson) L, O.

Strophomenacea: *Eopholidostrophia* sp. A, L; *Eostropheodonta* sp. H; *Furcitella* sp. L; *Katastrophomena* sp. L; *Leptaena aequalis* Amsden M; *Leptaena contermina* Cocks A; *Leptaena haverfordensis* Bancroft O; *Leptaena reedi* Cocks L, O; *Leptaena valentia* Cocks L; *Leptaena* sp. H, O, R; *Leptostrophia reedi* (Bancroft) A; *Leptostrophia* sp. L.

Davidsoniacea: *Fardenia* sp. G, L, R.

Porambonitacea: *Parastrophinella* sp. Z.

Pentameracea: *Clorinda malmoyensis* St Joseph Z; *Clorinda undata* (J. de C. Sowerby) H, L, O; *Clorinda* sp. R; *Stricklandia lens* (J. de C. Sowerby) H, L, O, R, Z; *Virgiana* sp. Z; *Virgianella sogdianica* Nikiforova & Sapelnikov Z.

Rhynchonellacea: *Rhynchotrema* sp. L; *Rhynchotreta*? sp. G.

Atrypacea: *Alispira gracilis* Nikiforova R; *Clintonella aprinis* (Verneuil) R; *Clintonella* sp. R; *Eospirigerina porkuniana* Rubel R; *Idiospira* sp. O; *Eospirigerina* sp. H, O, Z; *Meifodia recta alia* Nikiforova Z; *Meifodia* sp. L, O; *Plectatrypa imbricata* (J. de C. Sowerby) Z; *Plectatrypa* sp. L; *Protatrypa malmoeyensis* Boucot, Johnson & Staton O, Z; *Protatrypa* sp. M; *Protozyga* sp. L; *Zygospiraella* sp. M, Z; *Zygospiraella duboisi* (Verneuil) R.

Athyracea: '*Atrypina*' *gamachiana* Twenhofel A; *Cryptothyrella angustifrons* (Salter) L, G; *Cryptothyrella crassa* (J. de C. Sowerby) H, L; *Cryptothyrella* sp. A, R; '*Hindella*' *extenuata* Rubel R; *Hyattidina* sp. M.

From these lists it can be seen that the cited faunas carried 90 genera in the Hirnantian and only 54 in the early Rhuddanian, with 32 genera in common between the two lists. Part of this numerical discrepancy can be explained by the greater number of faunal lists available for beds of Hirnantian age (18), compared with only 8 for the early Rhuddanian; nevertheless that discrepancy can itself be explained by the fewer number of early Llandovery age faunas that can actually be found. Moreover, whereas the Hirnantian faunas can often be found in abundance (for example in China—Rong 1984*a*, *b*), the early Rhuddanian faunas are often very sparse both in numbers and diversity, and also in the actual size of the specimens, all of which explains why monographic treatment of them has been rather neglected, particularly by comparison with the much richer and more diverse later Rhuddanian faunas, which are relatively well described (e.g. Temple 1970). In addition, presumably because of the glacially-caused eustatic lowering of sea level which peaked during the Hirnantian, there are many sections in which only the Hirnantian is represented by shelly deposits and with the beds above and below in which the only macrofossils are graptolites.

Missing from both of the above lists are representatives of the Trimerellacea, Acrotretacea, Siphonotretacea and Chonetacea, all of which have reliable records from both late Ordovician and early Silurian rocks, but not from beds very close to the boundary; and from the early

Rhuddanian list the Craniacea and the Eichwaldiacea, which also yield representatives from later horizons in the Llandovery. The only brachiopod superfamily which appears to have become extinct at the end of the Hirnantian is the Gonambonitacea (although a few lower taxa such as the Trematidae also disappeared then); and the only new superfamily to appear anywhere near the base of the Silurian is the Cyrtiacea, whose earliest records, although not accurately dated in detail, come from beds in Tasmania extremely close to the boundary (Sheehan & Baillie 1981). In general, however, the degree of extinction across the boundary appears to have been far less than previously reported, largely because earlier studies have not concentrated on latest Ashgill and earliest Llandovery rocks. The extinctions at the end of the Hirnantian do not appear to have been greater than at the end Caradoc or end Rawtheyan. This is exemplified by a recent review of the atrypoids by Copper (1986), who states that only two genera, *Idiospira* and *Cyclospira*, may have become extinct near the boundary, and even these two have been reported (e.g. Baarli & Harper 1986) from early Silurian rocks. The strong 'Silurian' elements in the spire-bearer fauna, for example *Hindella* and *Eospirigerina*, actually appeared in late Rawtheyan times.

Unfortunately no evolutionary gradation within a single genus has been adequately studied across the boundary, and thus no perfect recognition of the boundary by brachiopods is yet possible. The most striking changes in closely related groups are seen in the Pentameracea, which can be found in virtually rock-building abundance in some beds both above and below the boundary, although only rarely in the earliest Rhuddanian. In the Hirnantian, *Holorhynchus*, *Brevilamnulella*, and others dominate the fauna, whereas in the Rhuddanian their place is taken by *Stricklandia*, *Clorinda*, and a wide diversity of genera in the then tropical areas of the USSR (Nikolaev *et al.* 1977) and, rather later, *Virgiana* and *Platymerella* in the USA. In the east Baltic, *Borealis* is known from as low as the *vesiculosus* Zone (Boucot *et al.* 1969).

The exact age, in terms of graptolite zones, of the various brachiopod faunas from near the systemic boundary, in particular the *Hirnantia* fauna, is also of great relevance in international correlation. In continuous sections, most *Hirnantia* faunas underlie beds bearing *persculptus* Zone graptolites, for example in the vast outcrop area in China, and in general the fauna is undoubtedly of *extraordinarius* Zone age or older; it spans four graptolite zones in China (Rong 1984*b*). However, in at least two places it occurs in beds with and above *persculptus* Zone graptolites. One is in Kazakhstan, USSR (Apollonov *et al.*, this volume, p. 145), and the other is in the Lake District, England, where Locality 74/1 of Hutt (1974: 15) in Yewdale Beck, Cumbria (National Grid ref. SD 3073 9858) has yielded to J. E. Hutt (registered numbers BC 7217–7236), in order of abundance, *Kinnella kielanae* (Temple), *Mirorthis mira* Zeng, *Plectothyrella crassicostis* (Dalman), *Cyclospira* sp., *Hirnantia* sp. and other indeterminate orthids and dalmanellids, identified by the author and Rong Jia-yu. In addition the same bed has yielded many graptolites (J. E. Hutt, pers. comm. 1986), including *Climacograptus medius* Törnquist, *C. normalis* Lapworth, *C. miserabilis* Elles & Wood, *Glyptograptus persculptus* (Salter), *Diplograptus* ex gr. *modestus* Lapworth and *Monograptus ceryx* Rickards & Hutt. These new records endorse the most preferable systemic boundary at the base of the *acuminatus* Zone.

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